ISSN 0753-4973

ALYTES



Décembre 1986

Volume 5, fascicule 4

SOCIÉTÉ BATRACHOLOGIQUE DE FRANCE

(Société pour l'Étude et la Protection des Amphibiens)

SIÈGE SOCIAL

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ALYTES

Bulletin trimestriel
Décembre 1986

Volume 5
Fascicule 4

Alytes, 1986, **5** (4) : 153-164.

Diets of tadpoles living in a Bornean rain forest

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Diets of 16 larval forms of Bornean anurans are generally similar to those of tadpoles from other regions : gut contents consist mainly of small algae and other protists. Despite broad overlap, there appear to be differences between diets of some co-occurring species in size and type of food ingested. Five feeding types are represented by these 16 kinds of tadpoles : obligate benthic, macrophagous, midwater suspension, surface film, and bottom suspension feeders. All except the last are associated with morphological specializations that appear to be functionally related to the size or kind of food particles ingested. Modes of feeding are related to differences in microhabitat distribution and to some of the differences in composition of the diets. It is this relationship that lends significance to food resource partitioning as an element in the organization of this Bornean tadpole community.

INTRODUCTION

Most of the recent spurt in non-taxonomic study of larval anurans, aside from developmental and neurobiology, has been focused on morphology and function of the buccopharynx (e.g., KENNY, 1969 ; SEALE & WASSERSUG, 1979 ; VIERTEL, 1985 ; WASSERSUG, 1980 ; WASSERSUG & HOFF, 1979) or on population ecology (e.g., HEYER, 1979 ; MORIN, 1983 ; WILBUR, 1984). Studies on the diets of free-living tadpoles are less numerous and usually concerned with one or two species (e.g., COSTA & BALASUBRAMANIAN, 1965 ; JENSSEN, 1967 ; SAVAGE, 1952 ; SEALE, 1980). HEYER (1973), who examined the gut contents of 17 larval forms in Thailand, found much overlap in the type of food ingested by tadpoles having keratinous beaks and denticles and a broader, though still overlapping, spectrum of food types in larvae lacking keratinous mouth



parts (Microhylidae). DIAZ-PANIAGUA (1985) related the modest differences among the diets of five species of tadpoles in Spain to differences in their distribution within the water column of ponds.

In this paper, I report observations on the diets of 16 species of tadpoles living in a Bornean rain forest at Nanga Tekalit, Sarawak. Twelve of these larval forms live in small streams where they occupy a variety of microhabitats : torrents around large boulders and rocks, shallow riffles over gravel, quiet open pools and areas of shingle rock, areas of leaf drifts trapped by eddies, shallow side pools cut off from the main current, and potholes in rocky banks. The remaining four larval forms live in pools distant from streams : either rain filled floor depressions made by forest pigs or tanks formed by anastomosing buttresses of three trunks. These 16 kinds of tadpoles are a subset of the 36 now known from Nanga Tekalit (INGER, 1985), occupy almost the entire array of microhabitats known to be used by tadpoles there, and represent 8 of the 14 genera.

This report has the nature of a preliminary survey. Sample sizes (see below) are not large enough to provide definitive descriptions of the larval diets of the individual species. However, even these limited samples reveal relationships among diet, morphology, and microhabitat distributions and the possibilities for food resource partitioning within a complex assemblage of tadpoles.

One of the difficulties in some studies of tadpole diets (and in the present one as well) is that objects identified as food may not be the actual sources of nourishment. Some protists, e.g., blue-green algae, other algae, *Volvox*, etc., are known to pass through the gut of tadpoles undamaged (COSTA & BALASUBRAMANIAN, 1965 ; SAVAGE, 1952). Conceivably, the true food may be bacteria or viruses, unseen and unrecorded, as suggested by HEYER (1973). Nonetheless, any systematic differences between species in either taxonomic category or size of items in the gut indicate at least differences in feeding habits.

MATERIALS AND METHODS

Processing of larvae in the field is described in INGER, VORIS & FROGNER (1986). To obtain samples of food, I cut half a centimeter of the foregut of a tadpole close to the esophagus and teased its contents on to a glass slide. I removed the gut wall and visible portions of its lining and added several drops of Melzer's solution (iodine and chloral hydrate). After spreading the gut contents as thinly as possible, I placed a cover slip over it and sealed the edges. I scanned the entirety of each smear within a few days of preparation, using a compound microscope equipped with an ocular grid.

Every item that was identifiably organic and had reasonably intact cell boundaries was measured (maximum diameter), recorded, and in the great majority of cases identified to major category (e.g., diatom, blue-green alga, fragment of tracheoid plant, etc.). It was not possible to identify food items to genus or species. About half of the cases in which identification was not possible involved small rod-like or spherical organic bodies that I classified as "protists."

Foregut smears were made from a total of 32 individuals. To minimize the risk of confounding differences between days or microhabitat sites with differences between species, wherever possible gut samples were taken from tadpoles of several species col-

Table I. — Microhabitat distribution, size, and stage of development of Bornean tadpoles used as sources of gut smears.

Species	Microhabitat	Stage*	Head-body length (mm)
	Tadpoles from stream microhabitats		
Leptobrachium gracilis	riffle	35	23
Leptobrachium montanum	shingle	26	19
	open pool	26	22
Megophrys nasuta	riffle	26	10
	shingle	34	11
Bufo divergens	side pool	37,37,39	7
Ansonia longidigita	leaf drift	36	5
Microhyla petrigena	pothole	29,35	4,7
Amolops phaeomerus	torrent	35,37	12,14
Rana blythi	leaf drift	26,39	7,10
	side pool	28	8
	pothole	26	8
Rana ibanorum	side pool	36	9
	pothole	28,33	8,10
Rana chalconota	side pool	26,28,40	8,14,15
Rana signata	leaf drift	38	13
Rhacophorus bimaculatus	riffle	36	9
	Tadpoles from microhabitats away from streams		
Microhyla borneensis	pig wallow	37	6
Rhacophorus dulitensis	pig wallow	27,36	16,17
Rhacophorus nigropalmatus	pig wallow	26	14
Rhacophorus harrissoni	buttress tank	27	11

*Stages according to GOSNER (1960).

lected on the same day at the same site. The following constituted such "multispecies" samples of foregut smears from cooccurring tadpoles :

— *Ansonia longidigita* + *Rana blythi,* 2 samples of each from leaf drifts ;
— *Bufo divergens* + *Rana chalconota,* 2 samples of each from side pools ;
— *Bufo divergens* + *Rana blythi* + *R. chalconota* + *R. ibanorum,* 1 sample of each from a side pool ;
— *Rana blythi* + *R. ibanorum,* 1 sample of each from a pothole ;
— *Microhyla borneensis* + *Rhacophorus dulitensis,* 2 samples of each from pig wallows.

Stages, sizes, and microhabitat sources of the tadpoles from which the food samples came are given in Table I.

Description of the general environment, full definitions of stream microhabitats, and microhabitat distributions of stream tadpoles appear in INGER, VORIS & FROGNER (1986) and descriptions of all larvae and definitions of non-riparian microhabitats in INGER (1985).

Table II. — Frequency distribution of food particles of various sizes in smears from foreguts of Bornean tadpoles. Number of smears per species given in Table I.

Species	Food particle size (mm)								
	<.03	.03-.05	.06-.10	.11-.15	.16-.20	.21-.30	.31-.40	>.4	mean*
				Tadpoles from stream microhabitats					
Leptobrachium gracilis	2	1	7	3	1	6	2	2	.132
Leptobrachium montanum		13	13	12	6	7	8	33	.188
Megophrys nasuta	36	8	10	3	1	11	4		.050
Bufo divergens	121	40	86	8	4	9			.041
Ansonia longidigita	34	30	13	1	1	1			.035
Microhyla petrigena	190	17	24	7	1	1	1		.026
Amolops phaeomerus	456	386	21	3	1	7			.029
Rana blythi	30	52	88	38	21	23	5	6	.080
Rana ibanorum	43	48	55	32	16	13	5	5	.069
Rana chalconota	117	51	36	14	8	11	4	7	.037
Rana signata	5	12	17	2	4	7		1	.075
Rhacophorus bimaculatus	40	34	1						.028
				Tadpoles from microhabitats away from streams					
Microhyla borneensis	2	15		5	2	1		1	.063
Rhacophorus dulitensis	12	73	48	28	8	7	1	10	.071
Rhacophorus harrissoni	29	7	52	8	10	20	3	4	.081
Rhacophorus nigropalmatus	10	10	73	13	6	6	1	1	.083

*Means calculated from class mid-points converted to logs. Assumed mid-point of smallest class = .02.

Differences in food size-frequency distributions were analyzed by means of the Kolmogorov-Smirnov test. The G test was used for comparing types of food, with unidentified items omitted.

RESULTS

Most of the gut samples include a wide spectrum of food types and sizes (Tables II and III). The community as a whole appears to be supported by a diet of very small organisms, mainly single-celled protists and short strands (usually <16 cells) of algae and fungi. Fragments of higher plants form the next most frequent category. There were also miscellaneous fragments of invertebrate cuticle, several butterfly scales, and pieces of arthropod exoskeleton.

The multispecies samples (see *Methods*) yield the following :

— *Ansonia longidigita* x *Rana blythi :* both sets show the same trend, i.e., food size smaller in *A. longidigita* ($P < .01$), and more tracheoid plant fragments eaten by *R. blythi* ($P < .001$).

— *Bufo divergens* x *Rana blythi :* food size smaller in *B. divergens* ($P = .005$) ; more tracheoid plant fragments eaten by *R. blythi* ($P < .001$).

Table III. — Frequency of food types in smears from foreguts of Bornean tadpoles. Number of smears per species given in Table I.

Species	Food types*										
	AL	DI	FN	CI	EU	AM	PR	TP	RO	MS	??
	Tadpoles from stream microhabitats										
Leptobrachium gracilis	1		3					13			7
Leptobrachium montanum	18		8					54		4	8
Megophrys nasuta	35	7	2					20		4	25
Bufo divergens	35	10	2	4	64		100	9		1	23
Ansonia longidigita	47	14		3				5			11
Microhyla petrigena					5		172	6		8	51
Amolops phaeomerus	807	12	2					3			38
Rana blythi	48	6	41	1	8	1		65		14	74
Rana ibanorum	75	7	39	9	1	2		24		7	48
Rana chalconota	90	14	16	1	7	2	108	23	3	2	44
Rana signata	15	5	5		1			6		2	13
Rhacophorus bimaculatus	43	32									
	Tadpoles from microhabitats away from streams										
Microhyla borneensis	10	1	6					3	1		3
Rhacophorus dulitensis	68	39	4	3	11	1	19	12	1	4	14
Rhacophorus harrissoni	13		20	2	1		49	22		5	21
Rhacophorus nigropalmatus	16	6	39	1	7	3	14	6	1	6	25

* AL = algae, mainly blue-green ; DI = diatoms ; FN = fungi ; CI = ciliates ; EU = euglenoids ; AM = amoebae ; PR = miscellaenous protists ; TP = tracheoid plant fragments ; RO = rotifers ; MS = miscellany, including insect and crustacean exoskeleton fragments ; ?? = unknown.

— *Bufo divergens* x *Rana chalconota :* food size smaller in *R. chalconota* in 2 sets ($P < .01$) but not the third ; no significant difference in type of food eaten.

— *Bufo divergens* x *Rana ibanorum :* food size smaller in *B. divergens* ($P < .001$) ; more tracheoid plant fragments eaten by *R. ibanorum* ($P < .001$).

— *Rana blythi* x *R. ibanorum :* food size smaller in *R. ibanorum* in one set ($P < .03$), but not in the other ; no significant difference in type of food eaten.

— *Rana blythi* x *R. chalconota :* no significant difference in size or type of food.

— *Rana ibanorum* x *R. chalconota* : no significant difference in size or type of food.

— *Rhacophorus dulitensis* x *Microhyla borneensis :* no significant difference in size or type of food eaten.

The 12 species from stream microhabitats fall into three groups on the basis of food particle size (Table II) : 2 (*Leptobrachium gracilis* and *L. montanum*) that fed on relatively large objects (mean particle size > .12 mm), with heavy emphasis on fragments of tracheoid plants ; 3 (*Rana blythi, R. ibanorum,* and *R. signata*) that had ingested a high proportion of medium-sized items (means .069-.08 mm) ; and 7 that contained a high proportion of very small items (means .026-.05 mm). For convenience I term these three groups macro-, meso-, and microphagous types, respectively. Differences within the microphagous group

are not significant (P >.10, Friedman 2- way ANOVA), but each of them differed significantly from each of the mesophages in pair-wise comparisons of food size-frequency distributions (P < .01, Kolmogorov-Smirnov test). However, I doubt the position of *Rana chalconota* with the microphagous species and the reality of the differences between it and *R. blythi* and *R. ibanorum* because of the results with multispecies samples (see above). The size-frequency distributions of the two species of *Leptobrachium* differ significantly (P <.05) in pair-wise tests with all others except for the *L. gracilis* x *R. signata* pair. The three mesophagous forms do not differ among themselves in size of food.

The two larval *Leptobrachium* are among the largest Bornean tadpoles (Table I and data in INGER, 1985) and have large beaks. They occur mainly in open pools (*L. montanum*) and riffles (*L. gracilis*). The three larval *Rana* constituting the mesophagous group are smaller (Table I) and have weaker beaks. One of them, *R. ibanorum*, lives primarily in side pools and potholes and the other two, *blythi* and *signata*, mainly in leaf drift.

The microphagous stream larvae are heterogeneous in size, phylogenetic relations, and ecological distribution. They include a small microhylid (*Microhyla petrigena*) lacking beaks and labial denticles, a medium-sized, funnel-mouth pelobatid (*Megophrys nasuta*), two small, generalized bufonids (*Ansonia longidigita* and *Bufo divergens*), a large, heavy-beaked ranid (*Amolops phaeomerus*), and a moderate-sized, heavy-beaked rhacophorid (*Rhacophorus bimaculatus*). The diversity of microhabitat distribution within this group is evident in Table I.

The four larval types collected away from streams do not differ significantly among themselves in size or general type of particles ingested. The rain-filled pig wallows in which three of them occurred had fine, silty bottoms and relatively few dead leaves. *Microhyla borneensis*, which we saw occasionally near the surface of the turbid water, is much smaller than the two rhacophorids (Table I) and lacked their horny beaks and denticles. We did not see the two rhacophorids near the surface unless we disturbed the water with nets. The buttress tank from which the sampled tadpole of *Rhacophorus harrissoni* came had a deep layer of dead leaves at the bottom.

DISCUSSION

MODES OF FEEDING

Direct observations on the behavior of free-living tadpoles provide information on where and roughly how seven forms feed : *Megophrys nasuta*, *Bufo divergens*, *Microhyla petrigena*, *M. borneensis*, *Amolops phaeomerus*, *Rana ibanorum*, and *R. chalconota*. In addition, we have reliable information on where in the water column nine additional forms spend most of their time and, presumably, where they feed : *Leptobrachium gracilis*, *L. montanum*, *Ansonia longidigita*, *Rana blythi*, *R. signata*, *Rhacophorus bimaculatus*, *R. dulitensis*, and *R. nigropalmatus*.

Five of the six modes of larval feeding defined by SATEL & WASSERSUG (1981) are recognizable in this community : (1) obligate benthic feeding, (2) creation of suspensions over the bottom (="generalist" of SATEL & WASSERSUG), (3) macrophagous, (4) midwater suspension feeding, and (5) particulate surface film feeding.

(1) Larval *Amolops phaeomerus* cling to rocks by means of an abdominal sucker and graze on the epilithic film of protists. The tadpoles are large enough to watch as they slowly move across rocks in clear water. *Rhacophorus bimaculatus*, which has a cup-like, suctorial oral disk, lives in the interstices of bottom rocks (INGER, 1985) and belongs in this category.

(2) Larval *Rana chalconota*, *R. ibanorum*, and *Bufo divergens* move slowly and irregularly over bottom debris in shallow side pools and potholes. Often an individual pauses in a snout-down, tail-elevated position, presumably creating and ingesting suspensions immediately above the interface of water and substrate. Larval *Rana blythi*, *R. signata*, and *Ansonia longidigita* live mainly within the layers of dead leaves that constitute leaf drifts and, given their gut contents, appear to feed by creating bottom suspensions. Larval *Rhacophorus harrissoni*, though living in tree buttress tanks, are like the preceding four species in living on and within mats of dead leaves. The broad spectrum of food types and sizes found in the sample from this species (Table II and III) suggests a similar mode of feeding. The two rhacophorids from pig wallows, *Rhacophorus dulitensis* and *R. nigropalmatus*, also appear to fit this feeding category.

(3) Larval *Leptobrachium montanum* and *L. gracilis* clearly ingest significant amounts of relatively large fragments of tracheoid plants (Table II and III). They apparently obtain much of their food by snipping off pieces of decaying vegetation. When larval *L. montanum* being reared in a field laboratory were offered dead leaves, they attacked the leaves around the margins, not on a broad surface.

(4) Only two larval types, *Microhyla borneensis* and *M. petrigena*, are midwater suspension feeders, a mode they share with other Asian microhylids (HEYER, 1973). *Microhyla petrigena* was easily and frequently observed in small, clear potholes with individuals distributed throughout the water column and remaining fixed in position unless disturbed. Although it was more difficult to see *M. borneensis* in the silty water of pig wallows, enough individuals were seen near the surface to suggest behavior similar to that of *M. petrigena*.

(5) *Megophrys nasuta* is the only larval form in this series that feeds at the surface film. Tadpoles of species of *Megophrys* have long been known to feed in this manner (e.g., SMITH, 1926 ; POPE, 1931 ; LIU, 1950).

MORPHOLOGICAL RELATIONS

Although this study did not involve critical investigation of functional relations, there appear to be some associations of oral and buccopharyngeal morphology with diets and mode of feeding for all except one group, those larvae that create and ingest bottom suspensions. The obligate benthic feeding *Amolops phaeomerus* and *Rhacophorus bimaculatus* share a number of features : (a) a suctorial device — an abdominal sucker in the former and the oral disk in the latter ; (b) heavy beaks with thick, coarse, marginal serrations and ribbed outer surfaces ; (c) long, scoop-shaped denticles sharply angled towards the mouth and having many marginal cusps (INGER, 1985 : fig. 33) ; (d) regular, pronounced decrease in size of denticles from inner to outer rows of both lips ; (e) modification of the anterior walls of the internal nares to form forwardly projecting flaps (INGER, 1985 : fig. 34) ; (f) no lingual papillae ; (g) few or no pustules in the interiors of buccal roof and floor arenas. Characters (a), (b), (d), (e), and (g) are unique to these two larval forms

among those dealt with in this paper. The form of their beaks and the length, angulation, and cusp wear pattern of their denticles suggest both these tadpoles use beaks and denticles to scrape rocks, which is consistent with their gut contents (Table III) and observed behavior of *A. phaeomerus*.

The macrophagous larval *Leptobrachium* have many rows of laterally compressed, sharply pointed denticles (INGER, 1985 : fig. 1) and very heavy, sharp beaks that seem suited to snipping bits of decaying vegetation. The array of large papillae in the buccal cavities of both *L. gracilis* and *L. montanum* (INGER, 1983) may serve to shunt large food particles away from the branchial baskets and glottis. Surface feeding *Megophrys* larvae hang from the surface film by means of their upturned funnel mouth (SMITH, 1926). LIU (1950) has described how the large palps and flaps just inside the mouth of *M. minor* act to block entrance of large objects. Similar structures occur in the buccal cavity of larval *M. nasuta* (INGER, 1985 : figs. 5-6), which has a much more slender beak than do tadpoles of other genera of Oriental pelobatids (see illustrations in POPE, 1931, and LIU, 1950). Mean food particle size is relatively small in *M. nasuta* (Table II). In common with other larval Microhylidae, the midwater suspension feeding tadpoles of *Microhyla borneensis* and *M. petrigena* lack beaks and denticles. Both have very large branchial baskets with dense filter ruffles (INGER, 1985 : fig. 16), suggesting filtration of small particles, though the food sample of only *petrigena* substantiates this suggestion (Table II). HEYER (1973) suggested that the method of feeding used by microhylid tadpoles is less discriminating both with respect to taxonomy and size of food items, but this idea is not borne out by the Bornean data (Tables II and III).

The tadpoles feeding on bottom suspensions are a mixture taxonomically and morphologically. Their morphological variation has no obvious functional or ecological correlation. The one feature they share — beaks of moderate thickness having finely serrated, sharp margins — is their only morphological distinction from all the other feeding types in this assemblage. Other morphological characters either vary widely within this group or overlap with one or several of the other feeding modes. For example, although all the bottom suspension feeders have many pustules (20-100) in the interior of buccal roof arena, so do the macrophagous larvae of *Leptobrachium*. Denticles of 5 of the 9 bottom feeders are set with many (> 12) triangular marginal cusps and have the end and sides of the shaft curved towards the mouth, features also found in the two obligate benthic feeders.

MICROHABITAT DISTRIBUTION

Modes of feeding and microhabitat distribution (Table I ; see also INGER, VORIS & FROGNER, 1986) are clearly related. The obligate benthic feeders are excluded from microhabitats, such as leaf drifts and silty side pools, where bottom cover would prevent development of the epilithic flora these tadpoles graze on. Bottom suspensions would be lost to tadpoles creating them in moderate or strong current, limiting distribution of this mode of feeding to standing water (e.g., pig wallows used by *Rhacophorus dulitensis*) or areas of weak current (e.g., side pools used by *Bufo divergens*). Similar physical constraints limit midwater suspension feeders to potholes along stream banks (*Microhyla petrigena*) or pools of standing water on the forest floor (*M. borneensis*). In contrast to the pre-

ceding types, the macrophagous *Leptobrachium* larvae are not restricted by either their basic food source, dead leaves, or their mode of feeding. However, only one of these larvae, *L. montanum*, actually has a wide microhabitat range (INGER, VORIS & FROGNER, 1986). Surface film feeding is apparently possible anywhere except in the most turbulent areas ; larval *Megophrys nasuta* used almost the entire range of stream microhabitats from riffles to potholes (INGER, VORIS & FROGNER, 1986).

TYPE OF FOOD

The dominant kinds of food in the diets of these Bornean tadpoles, as a group, resemble those of other assemblages. The main food source consists of small algae and other protists for larval communities investigated by SAVAGE (1952) in England, by HEYER (1973) in Thailand, by SEALE (1980) in Central United States, and DIAZ-PANIAGUA (1985) in Spain, as well as in the Bornean one. Interspecific variation within this framework can be described in only broad terms because of difficulties associated with specific identifications of food and with measurements and counts of food items. *Hyla meridionalis* and *Rana perezi* ingested much more Cyanophyta than the other three larvae from Spain (DIAZ-PANIAGUA, 1985). Diatoms were an important element in the food of all Thai larvae except those of *Kaloula pulchra* (HEYER, 1973). Cyanophyta were more important in gut contents of larval *Amolops phaeomerus* than in the other Bornean tadpoles (Table III).

Fragments of tracheoid plants were relatively common in both the Bornean (Table III) and Spanish assemblages (DIAZ-PANIAGUA, 1985), but were not reported for the Thai samples (HEYER, 1973). SAVAGE (1952) said that "higher plants appear to be almost useless as food for tadpoles..." because though "...eaten in large quantities by starving animals... [they]... do not support growth." SAVAGE's statement is probably related to the short time food is in the digestive tract of tadpoles (4-8 hrs in ones he studied) and the inability of tadpoles to break down cellulose (SAVAGE, 1952). Nonetheless, apparently healthy Bornean tadpoles ingest significant amounts of tracheoid plant matter, though they may be digesting microorganisms growing on those fragments.

Animal matter appeared only sporadically in food remains in all these samples, although SAVAGE thought that ingestion of micro-crustaceans had a significant positive effect on growth rates. SAVAGE interpreted "fairly common" appearance of tadpole denticles in the gut contents as evidence of feeding on dead larvae. Single denticles found in foregut smears of four Bornean tadpoles were clearly from conspecifics and indicate that tadpoles may sometimes swallow their own worn, shed denticles. This interpretation seems particularly apt for one of these four, a larval *Amolops phaeomerus*, for it is difficult to visualize how a tadpole of this species could feed on an object having the shape of a dead tadpole.

CONCLUSION

The role of diet in organizing tadpole communities has been minimized (HEYER, 1976 ; TOFT, 1985 ; DIAZ-PANIAGUA, 1985), partly because attention has centered on taxonomic composition of the diet. Given the overwhelming importance of protists as a food source for all these communities and the coarse level of food identification in most

studies, the observed high overlap between species in composition of the diet is expected. To be sure, the weak indications of specific differentiation (see above) might be strengthened by improved identifications of algae. However, that advance would be offset by the complications of temporal and microgeographic variation in algal blooms and microhabitat and temporal distributions of tadpoles. Differences among diets, in terms of size of food particles, exist (HEYER, 1973 ; this study, p. 156), although there is much overlap between species (Table II) and little relation to microhabitat distribution or larval size.

With improvements in measurement and identification of food and expansion of studies to other larval assemblages, composition of diets may ultimately help us understand organization of these communities. However, even with the present limitations of our data, it is evident that mode of feeding is an important factor in mediating the structure of tadpole communities (INGER, VORIS & FROGNER, 1986). HEYER's (1973) observation of three modes of feeding — bottom suspension feeders, midwater filter feeders, and surface film feeders — accounts for most of the variation in positions in the water column of the Thai tadpoles. The five feeding modes of the Bornean community (see p. 158) are related to differences in microhabitat distributions and to some of the differences in diet composition.

Those observations, however, leave an unanswered question : is the community structure that is revealed by diets, feeding modes, and microhabitat distributions maintained by ecological forces such as competition ? Differences among species within communities in modes of feeding and associated morphological specializations are correlated with taxonomic boundaries, at least in the Thai and Bornean samples, which have the largest arrays of species and genera. In Southeast Asia an abdominal sucker associated with obligatory benthic habits is confined to tadpoles of the genus *Amolops* and expanded suctorial lips limited to benthic feeding tadpoles of the *Rhacophorus bimaculatus* species group. Sharp beaks and compressed, knife-like denticles are found only in macrophagous pelobatid larvae (those of *Leptobrachium*, in this case) among Asian tadpoles. Surface feeding by means of "funnel" mouths is restricted to larval *Megophrys* and certain species of *Microhyla* in Southeast Asia, though these two groups have radically different buccopharyngeal structures (WASSERSUG, 1980) and presumably very different ways of processing food particles. Larvae of species groups (or subgenera) of Asian *Rana* show limited within-group morphological and behavioral variation (cf., HEYER, 1973 ; INGER, 1985 ; POPE, 1931). Given this broad correspondence between taxonomic boundaries and modes of feeding and morphology, the relation of feeding biology to organization of tadpole communities appears to owe more to phylogenetic events than to contemporary ecological forces.

ACKNOWLEDGEMENTS

I am grateful to Richard J. WASSERSUG for many stimulating discussions on the biology of tadpoles. Both he and Harold K. VORIS made helpful critical suggestions on the manuscript. Four colleagues, J. P. BACON, K. J. FROGNER, W. HOSMER, and F. W. KING, participated in the collection of tadpoles at various times. Field and laboratory work were partially supported by National Science Foundation grants G20867 and GB7845X and a grant from the Allen-Heath Memorial Foundation.

RÉSUMÉ

Les régimes alimentaires des têtards de 16 espèces d'Anoures vivant en forêt dense humide, à Bornéo, sont étudiés. D'une manière générale, ils s'avèrent similaires à ceux des têtards d'autres régions : les contenus digestifs sont principalement composés de petites algues et autres protistes. Malgré un large chevauchement, des différences sont constatées entre les régimes alimentaires de certaines espèces qui se rencontrent ensemble ; ces différences portent sur la taille et le type d'aliments ingérés. Cinq modes d'alimentation sont représentés parmi ces 16 types de têtards : l'alimentation benthique stricte, la macrophagie, l'alimentation à partir de particules en suspension en pleine eau, l'alimentation à partir du film en surface de l'eau et l'alimentation à partir de suspensions créées audessus du fond. Tous ces modes d'alimentation, sauf le dernier, sont associés à des modifications morphologiques qui sont en rapport fonctionnel avec la taille ou le type des particules alimentaires ingérées. A divers modes d'alimentation correspondent également des différences dans les microhabitats fréquentés par les têtards et certaines des différences observées dans la composition des régimes alimentaires. Ces corrélations indiquent que le partage des ressources alimentaires joue un rôle dans l'organisation de cette communauté de têtards de Bornéo.

(Résumé rédigé par J.-J. MORÈRE)

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Growth and metamorphosis of anuran larvae : effect of diet and temperature

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A diet that favours tadpole growth also quickens the onset of metamorphosis and promotes a greater transformation size. Within the range of 27°- 37°C metamorphosis is accelerated by increased temperature more than growth is and the larvae tend to transform at a lower size limit. At 15°C, growth was favoured over metamorphosis and the larvae grew beyond the normal upper limit showing a tendency toward facultative neoteny.

INTRODUCTION

Growth rate at each stage of development is an important part of a species life history strategy (COLE, 1954 ; GADGIL & BASSERT, 1970). In poikilothermic animals body size and growth rate are controlled by environmental conditions. Among aquatic animals body size and rate of growth are functions of the volume of water in which the animals are raised (HOGG, 1854 ; ALLEE, 1931) as well as of the more usual analyzed environmental factors of food supply and temperature. In general ectotherms grown at lower temperature are larger than those grown at higher temperature (HOWE, 1967 ; LOCK & MCLAREN, 1970).

Anuran metamorphosis, as a developmental process, involves both growth and differentiation and it is very difficult to separate the two processes. The concept of a metamorphic threshold size (WILBUR & COLLINS, 1973 ; SALTHE & MECHAM, 1974 ; DASH & HOTA, 1980 ; HOTA, 1984) indicates that conditions that affect the growth rate of larval anurans also affect the time of and body size at metamorphosis. In a study on the influence of food quality and quantity on early larval growth of two anuran species, STEINWASCHER & TRAVIS (1983) reported that growth was greatest at the highest ratio of protein to carbohydrate offered in the diet but not at the highest food level in *Hyla chrysoscelis*. However larval growth of *Rana clamitans* was unrelated to the specific protein / carbohydrate ratio in the diet but responded proportionately to change in protein content and food level. According to SMITH-GILL & BERVEN (1979), "environmental temperature is a major proximal factor in the growth, differentiation and overall life history patterns observed in amphibians". Given these considerations, in this study, we attempt to evaluate the effect of diet and temperature on growth and metamorphosis of *Rana tigerina* (Daudin) and *Bufo melanostictus* Schneider larvae.

METHODS

The methods of spawn collections were the same as described by HOTA & DASH (1981). The eggs were allowed to hatch in laboratory conditions and the hatchlings were mixed to assure uniformity in initial genetic and developmental conditions before being assigned at random to experimental treatment.

Experiments were started soon after the hatchlings begin to feed. Tap water, conditioned with sodium thiosulphate at a concentration of 8 mg/4.5 l (NACE & RICHARDS, 1972) and filtered, was used as the culture medium. According to GROMKO, MASON & SMITH-GILL (1973) the cube root of tadpole volume is the best estimator of larval size. MCNAB (1970) and BARTHOLOMEW (1977) argued in favour of weight as the best size measurement. In this study body mass has been used to estimate larval growth. Body mass was determined in a chemical balance sensitive to 0.001 g precision, by weighting one or more individuals (after blotted on a cloth towel) in a preweighed beaker containing 10 ml of clear distilled water. All weighings were done in duplicate.

The larvae were selected at random from the homogeneous population of both species and were assigned to the following experimental treatments.

(1) *R. tigerina* larvae in group of 5 and *B. melanostictus* larvae in group of 20, in triplicate sets were reared in different diets : (i) boiled *Amaranthus tricolor* leaves, (ii) boiled *Basella alba* leaves, (iii) cooked minced goat meat, (iv) boiled chicken egg yolk and (v) boiled *Amaranthus* leaves, boiled chicken egg yolk and cooked minced goat meat mixed in the proportion of 5 : 1 : 1. The larvae were fed *ad libitum*. Such food qualities were chosen with an aim to develop suitable culture method of anuran larvae and to produce healthy froglets and toadlets for dispersal as part of a frog farming programme.

(2) Groups of 5 and 20 of *R. tigerina* and *B. melanostictus* larvae, respectively, were reared at temperature 15°, 27°, 33° (room temperature in June and July) and 37°C with sufficient food (above mentioned diet type v).

The tadpoles in the experiments were allowed to progress to metamorphic climax stage. The emergence of first forelimb was taken as the criterion of onset of metamorphosis and complete resorption of tail was taken to indicate termination of metamorphic events. Metamorphosing individuals (froglets and toadlets with emergent forelimbs) were removed from the cultures into amphibious environments where they were allowed to complete metamorphosis to emerge as juveniles. The cultures were examined daily to determine the survival. The dead individuals were removed from the cultures and were excluded from analysis. Thrice weekly the culture pots were cleaned, water renewed and new food was added. Twice a week the masses of all larvae were determined to ascertain the mean growth rates. All statistical analyses were done according to SOKAL & ROHLF (1969).

RESULTS

GROWTH

A simple F, max test of the body mass of *R. tigerina* and *B. melanostictus* shows that the variances among groups reared in different diet are not significantly different (Tables I and II). But oneway analysis of variance indicates that the means are significantly different from one another (Tables I and II). A posteriori test suggests that each diet types are significant in their effects on growth of *R. tigerina* larvae (Table I), whereas the effects

Table I. — Test of variances among *R. tigerina* larvae after 15th days growth as a function of different diet.

Nos.	Diet	Average body weight (g)	S.D.
1.	Boiled *Amaranthus tricolor* leaves	0.1690	0.0042
2.	Boiled *Basella alba* leaves	0.2138	0.0093
3.	Cooked minced goat meat	0.2746	0.0296
4.	Boiled egg yolk	0.3600	0.0147
5.	Mixed diet	0.4412	0.0151
	F, max = 75.53 (ns)		

Anova table

Variation	df	S.S.	M.S.	F.
Treatments	4	0.30415	0.07604	267.45 **
Error	10	0.00284	0.00028	
Total	14	0.30699		

Coeff. det. = R^2 = 0.98
** Significant at 0.001 level

A posteriori test (S.N.K. test)

	2	3	4	5
Q	3.15	3.88	4.33	4.66
L.S.R.	0.0304	0 0374	0.0418	0.045

1 < 2 < 3 < 4 < 5

of each pair of diet types on growth of *B. melanostictus* larvae are similar (Table II). It is evident that the final mass of larvae of both the species increased with the supplemented carnivorous diet. After 35th day of rearing with a strictly plant diet, heavy mortality and deformities were observed amongst *R. tigerina* larvae.

At lower temperature the larvae of both species were larger at any given stage (fig. 1). The apparent decline in weight at 15°C in both species was due to heavy mortality of larger animals causing a drop in the average weight.

METAMORPHOSIS

Table III summarises the effect of diet on size and time of metamorphosis. In exclusively plant diet, not a single *R. tigerina* larva from the replicate pots developed forelimbs. In contrast *B. melanostictus* larvae reached metamorphic climax at around the 15th day after hatching with all diets tested in this experiment. But there was distinct varia-

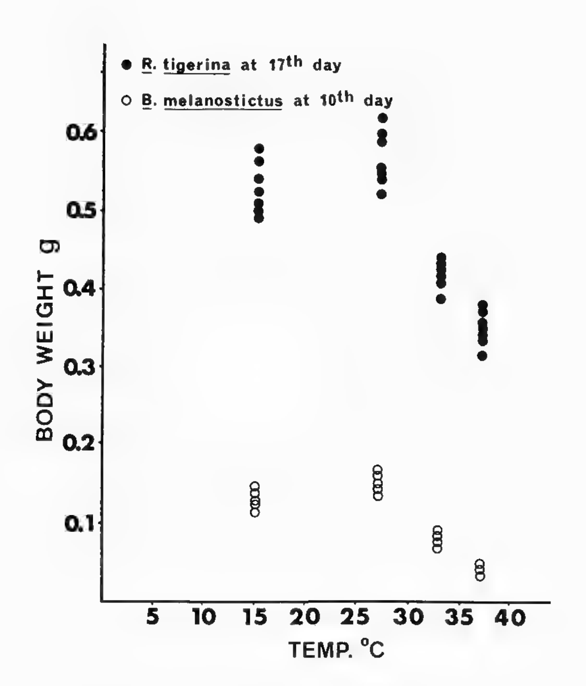


Fig. 1. — Temperature dependent growth of individual *R. tigerina* and *B. melanostictus* larvae.

Table II. — Test of variances among *B. melanostictus* larvae after 10 days growth as a function of different diet.

Nos.	Diet	Average body mass (g)	S.D
1.	Boiled *Amaranthus tricolor* leaves	0.086	0 017
2.	Boiled *Basella alba* leaves	0.096	0.007
3.	Cooked minced goat meat	0.109	0.009
4.	Boiled chicken egg yolk	0.120	0.005
5.	Mixed diet	0.137	0.008

F, max = 75.53 (ns)

Anova table

Variation	df	S.S.	M.S.	F.
Treatments	4	0.00485	0.001213	11.79**
Error	10	0.00103	0.000103	
Total	14	0.00588		

Coeff. det. = R^2 = 0.83
** Significant at 0.01 level

A posteriori test (S.N.K. test)

	2	3	4	5
Q	3.15	3.88	4.33	4 66
L.S.R.	0 0184	0.0227	0.0253	0.0273

1 < 2 < 3 < 4 < 5

tion in metamorphic size. A comparison of Tables I, II and III suggests that the diet that favours growth also favours quickening of the onset of metamorphic events and promotes a greater size at transformation.

Table IV enumerates the effect of temperature on the time of metamorphosis and metamorphic size. Within the range of 27° to 37°C lower temperature favoured greater transformation size in both species. But the larvae reared at 15°C grew for a long time into giant larvae and did not metamorphose, developing neotenic tendency. Ultimately they could not adapt to permanent neoteny and died.

DISCUSSION

In frogs and toads there is usually a drastic change from aquatic herbivory to terrestrial carnivory, demanding reorganization of the gut during metamorphosis. *Rana tigerina* undergoes a "first metamorphosis" in the middle of its larval life when it changes from being a herbivore to being a carnivore (VARUTE, 1970). Probably because of this first metamorphosis in the middle of larval life, the growth of the *R. tigerina* larvae with

Table III. — Metamorphic size and the time of metamorphosis as a function of diet

Diet	*R. tigerina*		*B. melanostictus*	
	$\overline{X}$ (g) ± S.D.	Time in days	$\overline{X}$ (g) ± S.D.	Time in days
Boiled *A. tricolor* leaves	Did not metamorphose		0.129 ± 0.007	15
Boiled *B. alba* leaves	-do-		0.144 ± 0.006	15
Cooked minced goat meat	0.751 ± 0.016	34	0.164 ± 0.009	15
Boiled egg yolk	0.755 ± 0.026	28	0.180 ± 0.008	15
Mixed diet	0.855 ± 0.025	28	0.215 ± 0.011	15

Table IV. — Metamorphic size and time of metamorphosis as a function of temperature.

Temperature °C	*R. tigerina*		*B. melanostictus*	
	$\overline{X}$ (g) ± S.D.	Time in days	$\overline{X}$ (g) ± S.D.	Time in days
37	0.750 ± 0.035	28	0.130 ± 0 009	16
33	0.858 ± 0 016	28	0 137 ± 0.002	15
27	0.050 ± 0.048	29	0.169 ± 0.012	15
15	Did not metamorphose.After 64th day high rate of mortality was observed and experiment was discontinued.		Did not metamorphose. After 48th day high rate of mortality was observed and experiment was discontinued.	

plant diets is checked and they cannot attain the minimum threshold size for completing the second metamorphic step. In nature, this does not happen. *R. tigerina* larvae can satisfy their carnivorous habits with a variety of insect larvae or other microinvertebrate prey during this period. So in this study the mixed diet gave best results. In contrast, the gut reorganization in the larvae of *R. clamitans* occurs after the emergence of the forelimbs, when they stop feeding (JENSSEN, 1967). In this case the first and second metamorphic processes are not distinguishable. In our experiment *B. melanostictus* larvae behaved like *R. clamitans,* so that the plant diet did not affect the transformation as the gut reorganization which occurs after metamorphosis is initiated.

In this study the results with controlled temperature follow the trend reported for *R pipiens* by SMITH-GILL & BERVEN (1979). Here also, the results show that the environmental temperature is a major proximal factor in the growth of *R. tigerina* and *B. melanostictus* larvae. As in the case of *R. pipiens* (SMITH-GILL & BERVEN, 1979) either direct temperature effects on the developing tissue or indirect temperature effect mediated by thyroxine, are sufficient to explain temperature dependence of growth in these two species.

It has been shown that metamorphosis and the effects of thyroid hormones on other species tadpoles are completely inhibited below temperature 5°C (HUXLEY, 1929 ; LYNN & WACHOWSKI, 1951 ; FRIEDEN, WAHLBORG & HOWARD, 1965 ; ASHLEY, KATTI &

FRIEDEN, 1968). Similarly, in this study metamorphosis is inhibited at 15°C. The tropical climate of Sambalpur provides a mean daily temperature of 20°C in winter, 30°C in summer (maximum being 42°- 45°C), and also 30°C in the rainy season. So this rise in the lower temperature tolerance of metamorphic process of *R. tigerina* and *B. melanostictus* might be a compensatory adaptation to tropical climate. The length of the larval stages of the American bull frog in nature increases with the length and severity of the winters (WILLIS, MOYLE & BASKETT, 1956). ETKIN (1964) has observed that within the range of 15°- 30°C metamorphosis is accelerated by increased temperature and the animals metamorphose at a small size. This appears to be partly true also with *R. tigerina* and *B. melanostictus*. In this study, within the range of 27°- 37°C the lower temperature favoured transformation at a greater size and higher temperature hastens the initiation of metamorphic events and favours the transformation at a lower size. However, in this investigation unlike that of the American bull frog, there is no significant increase in the larval period at low temperature.

ACKNOWLEDGEMENT

The authors wish to thank Dr. Ian MCLAREN for his critical comments. Financial support for this study from University Grants Commission, New Delhi (Grant No. 057/Bio-Scs/76) is greatefully acknowledged.

RÉSUMÉ

L'influence de l'alimentation et celle de la température sur la croissance et la métamorphose des larves d'Anoures sont étudiées à partir d'expériences effectuées sur *Rana tigerina* et *Bufo melanostictus*. Cinq types de régimes alimentaires (composés uniquement de végétaux, de viande, de jaune d'œuf, ou mixte) sont testés. Les meilleurs résultats sont obtenus avec un régime mixte. Une alimentation qui favorise la croissance des têtards a pour effet également d'accélérer le déclenchement de leur métamorphose et d'entraîner une plus grande taille des métamorphosés. Entre 27° et 37°C un accroissement de la température accélère l'apparition de la métamorphose plus que la croissance larvaire de sorte que les têtards ont tendance à se transformer à une taille inférieure. A 15°C la croissance est favorisée aux dépens de la métamorphose de sorte que les larves grandissent au-delà des valeurs limites habituelles et qu'elles manifestent une tendance vers la néoténie facultative.

(Résumé rédigé par J.-J. MORÈRE)

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Alytes, 1986, **5** (4) : 173-174.

Miscellanea nomenclatorica batrachologica (XIV)

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The family-group name "Oreolalaxinae" Tian & Hu, 1985, which should be emended to Oreolalaginae, is a strict synonym of Leptobrachiinae Dubois, 1980. This subfamily includes the genera and subgenera *Leptobrachium*, *Leptolalax*, *Scutiger*, *Oreolalax*, *Aelurolalax*, and also *Leptobrachella*, which was erroneously placed by TIAN & HU (1985) in the Megophryinae.

TIAN & HU (1985) ont proposé la création d'une nouvelle sous-famille des Pelobatidae, regroupant les genres (ou sous-genres) *Leptobrachium*, *Leptolalax*, *Scutiger*, *Oreolalax*. Pour cette sous-famille, ils ont créé le nom "Oreolalaxinae", fondé sur le nom générique *Oreolalax*.

Il faut tout d'abord noter que le nouveau nom de sous-famille est mal formé, et doit être émendé en "Oreolalaginae". En effet le nom *Oreolalax* est fondé sur le mot grec λάλαξ, dont le génitif est λάλαγος, et le radical de ce nom générique est donc *Oreolalag-*.

De toute manière, ce nom du groupe-famille n'aura pas lieu d'être utilisé, car il s'agit d'un strict synonyme plus récent du nom Leptobrachiinae Dubois, 1980. Ce dernier nom fut d'abord proposé (DUBOIS, 1980 : 471) sous la forme Leptobrachiini, pour la tribu regroupant les genres à têtards "généralisés" des Megophryinae, opposée à la tribu des Megophryini, dont les têtards ont une bouche en entonnoir. Ce taxon fut élevé au rang de sous-famille Leptobrachiinae par DUBOIS (1983 a : 272), et mentionné à diverses reprises par la suite (DUBOIS, 1983 b : 147-148, 1984 : 29, 1985 : 74, 1987 : 13 ; FROST, 1985 : 409).

Notons enfin que c'est à tort que TIAN & HU (1985) incluent le genre *Leptobrachella* dans la sous-famille des Megophryinae : le têtard de *Leptobrachella mjobergi* décrit en détail par INGER (1983) s'avère très proche des têtards de *Leptolalax*, ce qui indique que la place de *Leptobrachella* est au sein des Leptobrachiinae.

Les Leptobrachiinae comportent donc les genres et sous-genres suivants (DUBOIS, 1987) : *Leptobrachium* Tschudi, 1838 (dont *Vibrissaphora* Liu, 1945 est synonyme) ; *Leptolalax* Dubois, 1980; *Leptobrachella* Smith, 1925 ; *Scutiger* Theobald, 1868 ; *Oreolalax* Myers & Leviton, 1962 ; et *Aelurolalax* Dubois, 1987.

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Miscellanea nomenclatorica batrachologica (XV)

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The generic name *Ranixalus* Dubois, 1986 is a synonym of *Indirana* Laurent, 1986, which was proposed independently and published a few months earlier. The name Ranixalini Dubois, 1987 remains the valid name for the tribe which includes *Indirana*, *Nyctibatrachus* and *Nannophrys*.

Nous avons récemment (DUBOIS, 1986) décrit sous le nom *Ranixalus gundia* une nouvelle espèce de Ranoidea du Karnataka, dont nous avons ensuite (DUBOIS, 1987) montré qu'elle appartenait à un genre de Ranidae endémique du sud de l'Inde, comprenant *Polypedates beddomii* Günther, 1876 et les espèces voisines. Pour ce genre, nous avons initialement (DUBOIS, 1987) retenu le nom *Ranixalus* Dubois, 1986, mais le nom générique *Indirana* Laurent, 1986, proposé indépendamment et publié quelques mois plus tôt par LAURENT (1986 : 761) pour *Polypedates beddomii* et les espèces voisines, s'avère avoir priorité. Toutes les espèces placées par DUBOIS (1987) dans le genre *Ranixalus* doivent donc être rapportées au genre *Indirana*. Notons toutefois que quelques-unes des espèces rapportées par LAURENT (1986) à ce genre appartiennent en fait à d'autres genres (pour plus de détails, voir DUBOIS, 1987).

A l'examen des descriptions et figures que GUNTHER (1876) et INGER et al (1984) ont donné de *Indirana brachytarsus* (Gunther, 1876) il nous paraît que cette espèce pourrait être la même que *Indirana gundia* (Dubois, 1986), mais jusqu'à présent nous n'avons pas eu la possibilité d'examiner les types de *Polypedates brachytarsus*, ou d'autres spécimens rapportés à cette espèce.

En ce qui concerne enfin la nomenclature supragénérique, la mise en synonymie de *Ranixalus* n'implique nullement la nécessité d'abandonner le nom Ranixalini Dubois, 1987, qui reste le nom valide de la tribu comportant les genres *Indirana*, *Nyctibatrachus* et *Nannophrys* (voir DUBOIS, 1987).

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REFEREES

The editors of *Alytes* thank warmly the following colleagues, who accepted to read, study and comment the papers submitted for publication in *Alytes* from 1st July 1985 to 30 June 1987:

Edouard-Raoul BRYGOO (Paris)

Stephen D. BUSACK (Urbana)

Ronald I. CROMBIE (Washington)

William E. DUELLMAN (Lawrence)

Carl GANS (Ann Arbor)

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ALYTES

Journal International de Batrachologie
International Journal of Batrachology

édité par la Société Batrachologique de France

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Publié avec le concours du Muséum national d'Histoire naturelle.

Directeur de la Publication : Alain DUBOIS.

Numéro de Commission Paritaire : 64851.

Alytes, 1986, **5** (4) : 153-176.

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Photocomposition/Photogravure : Alexandre, Paris. 42 46 17 57.
Imprimé aux Ateliers de la Couronnerie, 45750 Saint-Pryvé Saint-Mesmin, France.
Dépôt légal : 3ᵉ trimestre 1987.